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SYSTEMATIC IMPLICATIONS OF CHROMOSOMAL BANDING ANALYSES OF POPULATIONS OF *PEROMYSCUS TRUEI* (RODENTIA: MURIDAE)

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Abstract.—C-band, G-band, and Ag-NOR analyses were carried out on the southern (AN = 54) and northern (AN = 62) cytotypes of *Peromyscus truei* from New Mexico, Texas, and Oregon. Results support the retention of *comanche* as a subspecies of *P. truei,* but populations possessing the southern cytotype are regarded as specifically distinct and referable to *Peromyscus gratus.*

Peromyscus truei, as currently recognized, contains 15 subspecies including *Peromyscus truei comanche* (Hall 1981; Schmidly 1973). This arrangement differs somewhat from the latest taxonomic revision of the species (Hoffmeister 1951), which recognized 12 subspecies and regarded *comanche* as a subspecies of *Peromyscus nasutus* (=*P. difficilis*).

Several karyological studies have addressed the systematics and evolution of *P. truei.* These analyses indicate that two distinct chromosomal forms exist: a northern, 2n = 48, AN = 62 cytotype (AN = number of autosomal arms, see Lee and Elder 1977) from the western and southwestern United States, and a southern, 2n = 48, AN = 54 cytotype from New Mexico and Mexico (Hsu and Arrighi 1968; Lee *et al.* 1972; Zimmerman *et al.* 1975). Further, the standard karyotype of *P. t. comanche* was shown to be identical to that of *P. truei* and quite different from that of *P. difficilis* (Lee *et al.* 1972).

We present chromosomal banding comparisons of *P. t. comanche* and of the two *P. truei* cytotypes. We think the evidence derived both from our work and from previous studies most appropriately maintains *P. t. comanche* as a subspecies of of *P. truei,* while we recognize populations having the southern, AN = 54 cytotype as a distinct species referable to *P. gratus* Merriam, 1898.

Methods.—Mice were live-trapped and shipped to the laboratory for processing. All chromosomal preparations were derived from bone marrow following Lee and Elder (1980). The differential staining procedures we utilized are also cited therein. Voucher specimens are deposited in the Museum of Natural History, University of Illinois, Urbana-Champaign.

Specimens examined: *P. t. truei* (12), New Mexico: 2 mi NE Hanover, Grant Co., 1 female; 2 mi N Hanover, Grant Co., 2 males, 1 female; 8 mi S Magdalena, Socorro Co., 2 males, 1 female; 1 mi N Magdalena, 2 males; 2 mi up from Monica Canyon Ranger Station, San Mateo Mts., Socorro Co., 2 males, 1 female. *P. t. comanche* (4), Texas: 15 mi E Canyon, Randall Co., 3 males, 1 female. *P. t. preblei*

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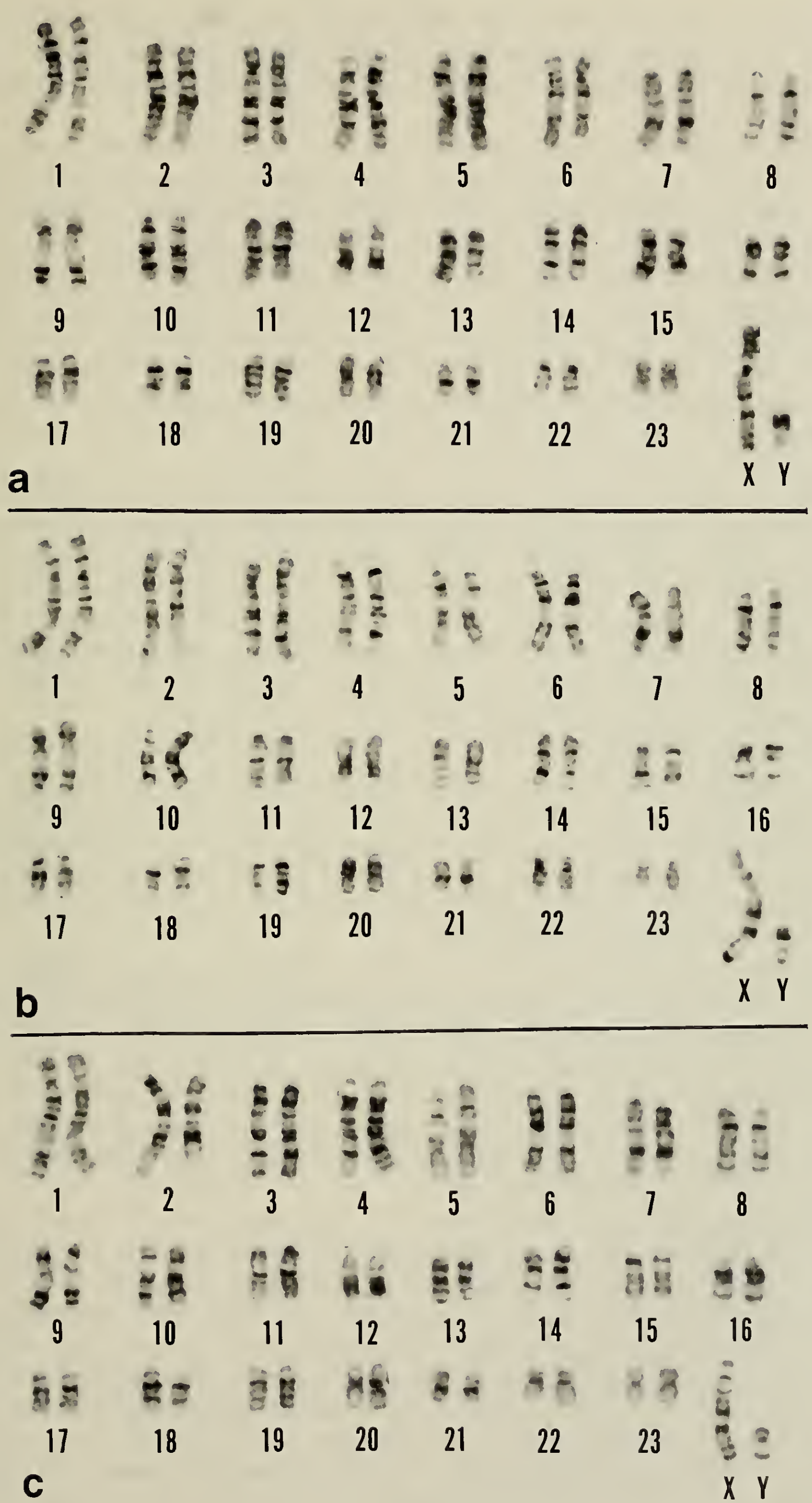
Fig. 1. a, G-banded karyotype of *P. t. truei.* Autosomes and X chromosome are from a female, the Y chromosome is from a male; b, G-banded karyotype of a male *P. t. comanche*; c, G-banded karyotype of a male *P. gratus.*


1 2 3 4 5 6 7 8
9 10 11 12 13 14 15
17 18 19 20 21 22 23
X Y
a
1 2 3 4 5 6 7 8
9 10 11 12 13 14 15 16
17 18 19 20 21 22 23
X Y
b
1 2 3 4 5 6 7 8
9 10 11 12 13 14 15 16
17 18 19 20 21 22 23
X Y
c

(3), Oregon, 10 mi NW Terrebonne, Jefferson Co., 3 females. *P. gratus* (4), New Mexico: 2 mi NE Hanover, Grant Co., 1 female; 1 mi N Luna, Catron Co., 1 male; 3 mi up from Monica Canyon Ranger Station, San Mateo Mts., Socorro Co., 2 males.

Results.—Peromyscus truei truei (2n = 48, AN = 62). All autosomes are acrocentric except 1, 2, 3, 6, 9, 15, 22, and 23. The X is a large submetacentric; the Y is a small acrocentric. The short arm of chromosome 1 is longer than that found thus far in other *Peromyscus* and appears to be the result of a pericentric inversion not involving the telomere (Figs. 1a, 3d). Autosomal heterochromatin is restricted to centromeric regions. The centromeric area and short arms of the X and the proximal one-third to one-half of the Y are heterochromatic (Fig. 2a). Our G- and C-band results appear to agree with those of Robbins and Baker (1981) for this species, although they apparently misidentified pairs 16, 17, 18, and 20 (see Committee 1977, Fig. 1a). Nucleolus organizer regions (NORs) are located telometrically on the short arms of pairs 1 and 22 (Fig. 3c).

Peromyscus truei comanche (2n = 48, AN = 62). The karyotype is similar to that of *P. t. truei*. The elements within the G-banded karyotype of *P. t. comanche* and *P. t. truei* are homologous with the exception of the short arms of chromosome 6 and the X (Figs. 1b, 3d). These differences were not observed by Robbins and Baker (1981) in their examination of *P. t. comanche*. The chromosomal locations of C-bands are the same as in *P. t. truei*; however, the amount of heterochromatin in the karyotype of *P. t. comanche* is somewhat less (Fig. 2b). The silver-stained karyotype is indistinguishable from that of *P. t. truei* (Fig. 3a).

Peromyscus truei preblei (2n = 48, AN = 62). The elements within the G-banded karyotype are homologous with those of *P. t. truei* and *P. t. comanche*, again with the exception of the short arms of chromosome 6 and the X (Fig. 3d). Each of the three populations of *P. truei* thus possesses different G-banding patterns for these two elements. The C-banded karyotype (not shown) is similar to that of *P. t. comanche*, and the silver-stained karyotype (also not shown) is identical to those of *P. t. truei* and *P. t. comanche*.

Peromyscus gratus (2n = 48, AN = 54). All autosomes are acrocentric except pairs 1, 2, 22, and 23. The X is a large submetacentric; the Y is a small metacentric. The Y chromosome and the short arm of the X have unique G-band patterns compared with other species of *Peromyscus* (Figs. 1c, 3d). (See Greenbaum *et al.* 1978; Robbins and Baker 1981; Yates *et al.* 1980). Heterochromatin is located centromerically on all autosomes and the sex chromosomes, and on the short arms of the Y (Fig. 2c). Three pairs of Ag-NORs are located telomerically on pairs 3, 7 or 8 or 9, and 22 (Fig. 3b).

Discussion.—Peromyscus truei truei, *P. t. comanche*, and *P. t. preblei*, differ karyotypically in the inversion patterns found in chromosome 6, in the G-banding patterns of the heterochromatic short arm of the X, and in the presence of slightly more heterochromatin in the karyotype of *P. t. truei*. These findings indicate that *P. t. comanche* has undergone only a slight amount of chromosomal change in the 10,000-year period that it has been geographically isolated from the main population of *P. truei* (Blair 1950), and is no more differentiated than are either of the other two populations that were examined. We think that *P. t. comanche* should be retained as a subspecies of *P. truei*. This same conclusion was reached by Schmidly (1973) using morphological criteria. Electrophoretic comparisons of

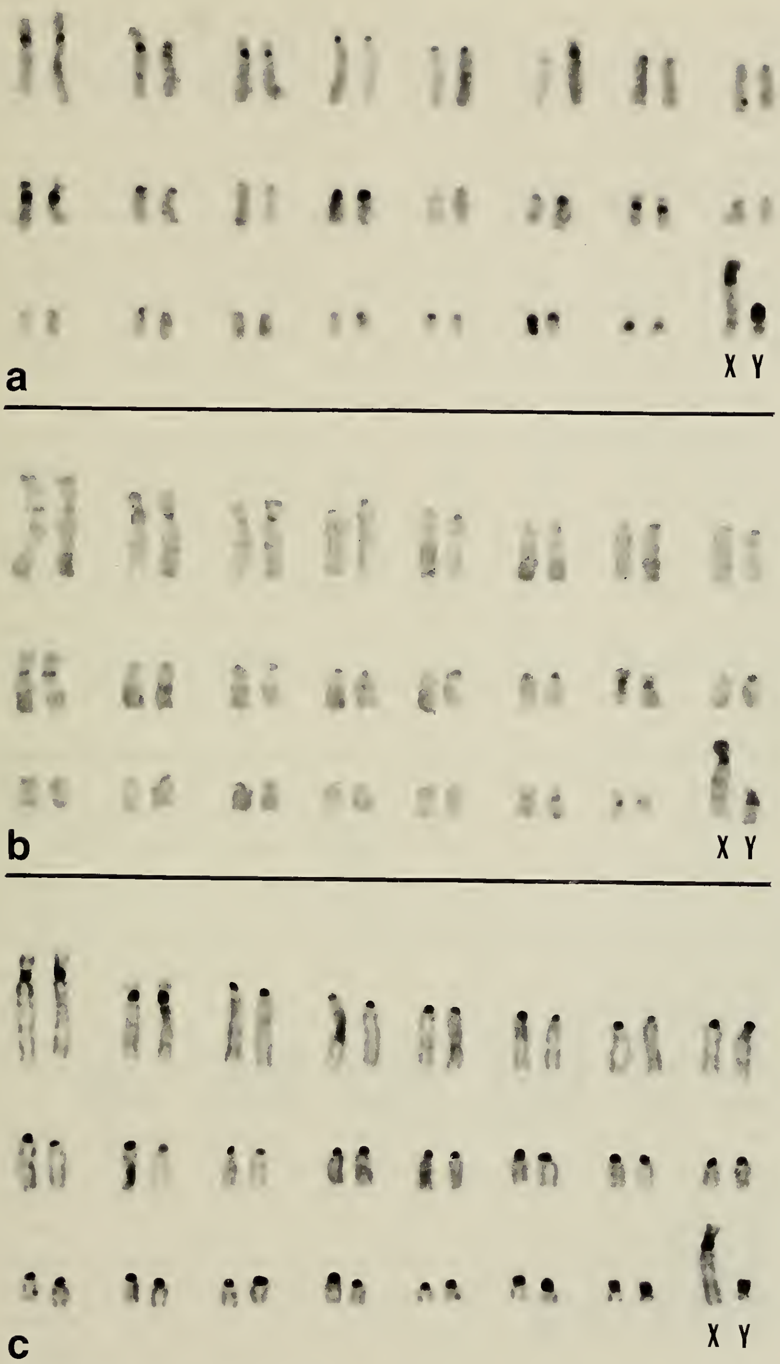


Fig. 2. a, C-banded karyotype of a male *P. t. truei*; b, C-banded karyotype of a male *P. t. comanche*; c, C-banded karyotype of a male *P. gratus*.

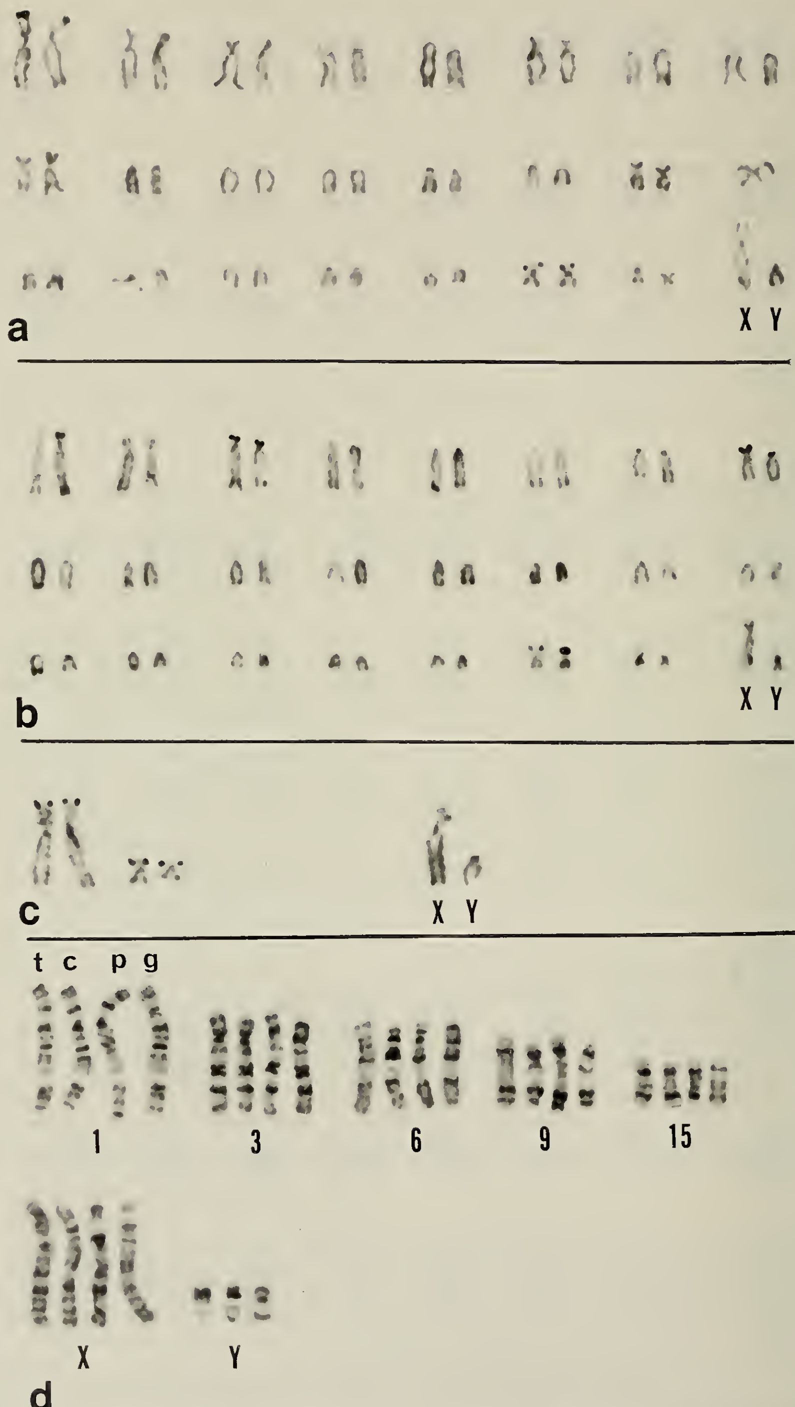


Fig. 3. a, Silver-stained karyotype of a male *P. t. comanche*; b, Silver-stained karyotype of a male *P. gratus*; c, Partial silver-stained karyotype of a male *P. t. truei* showing two pairs of autosomes with Ag-NORs and the sex chromosomes; d, Partial, composite, G-banded karyotype (*P. t. truei* (t), *P. t. comanche* (c), *P. t. preblei* (p), *P. gratus* (g), from left to right in each set) showing elements for which G-band differences exist among the four taxa. The Y was not examined in *P. t. preblei*.

P. truei truei and *P. t. comanche* (Rogers' similarity = 0.96, Johnson and Packard 1974) also suggest to us no more than subspecific differentiation of *commanche*; Johnson and Packard (1974), however, recommended specific status for *comanche*. Unpublished data from breeding experiments in our laboratory also show that *P. truei truei* (New Mexico) and *P. t. comanche* are completely interfertile.

The problem regarding *P. truei* and *P. gratus* is more complex. Karyotypic data from conventional and banded preparations are available for 122 specimens belonging to these two taxa. Seventy-five individuals (AN = 62) have been examined from Utah and California (Hsu and Arrighi 1968); Arizona, Colorado, Utah, and Texas (Lee *et al.* 1972); New Mexico and Texas (Robbins and Baker 1981; present study); Oregon (present study); and Arizona, Utah, and New Mexico (Zimmerman *et al.* 1975). Forty-seven specimens (AN = 54) have been reported from New Mexico (Hsu and Arrighi 1968; present study), Coahuila (Lee *et al.* 1972), Chihuahua and Durango (Zimmerman *et al.* 1975), and Michoacan and Mexico (Schmidly and Kilpatrick, pers. comm.).

No karyotypic variation has yet been reported within either cytotype with the exception of the differences reported here between *P. t. truei, P. t. comanche* and *P. t. preblei*. Most importantly, near and at the contact zone of the AN = 62 and the AN = 54 cytotypes in New Mexico, 24 specimens have been collected which range from being fully sympatric to occurring within 20 miles of one another in Grant and Socorro Counties, and none was karyotypically intermediate (Hsu and Arrighi 1968; Robbins and Baker 1981; Zimmerman and Kilpatrick 1972; present study).

When the cytotypes of *P. truei* and *P. gratus* are compared at least five major chromosomal differences can be demonstrated: (1) based on the primitive *Peromyscus* karyotype proposed by Robbins and Baker (1981) *P. truei* has undergone pericentric inversions in chromosomes 1, 2, 3, 6, 9, and 15, whereas *P. gratus* has experienced an inversion only in chromosome 2 (although we tentatively follow Robbins and Baker, 1981, who designated euchromatic differences of this type as pericentric inversions, we think that latent centromeric activity rather than inversions may account for at least some of these differences in euchromatic arm morphology, e.g., chromosome 3); (2) significant differences are seen in the G-banded and C-banded patterns of the short arms of the X chromosomes; (3) major differences exist in the morphology and in the G- and C-band patterns found in the Y chromosomes; (4) a difference occurs in the number and location of Ag-NORs; and, (5) there is a difference in the total amount of autosomal heterochromatin; more C-band positive material is found in *P. gratus*. Since both of the cytotypes are distinctive, wide-ranging, relatively homogeneous, and occur sympatrically, in our opinion each warrants recognition as a distinct species. Electrophoretic comparisons of *P. truei* and *P. gratus* yielded values (S = 0.866, 0.872, Avise *et al.* 1979; S = 0.863, Zimmerman *et al.* 1975) that are representative of those found between some species or semispecies of *Peromyscus* (Avise 1975; Zimmerman *et al.* 1978).

The northern limits of the geographic distribution of *P. gratus* are not precisely known. In his revision of *P. truei,* Hoffmeister (1951:29) recognized a subspecific boundary between *P. t. truei* and *P. t. gentilis* that closely coincided with the United States-Mexican border. However, the presence of *P. gratus* in New Mexico, as well as in Mexico, indicates that the limits of *P. gratus* should be extended northward at least to central and southern New Mexico. The distribution of *P.*

gratus thus includes the present ranges of *P. t. gratus, P. t. gentilis, P. t. erasmus, P. t. zapotecae,* and part of *P. t. truei.* The remaining northern populations and subspecies represent *P. truei* (see Hall 1981:702).

Systematics and Synonymy

Peromyscus gratus Merriam
Peromyscus gratus erasmus Finley

Peromyscus truei erasmus Finley, 1952, University, Kansas Publications, Museum Natural History, 5:625. Type from 8 mi NE Durango, 6200 ft., Durango.

Peromyscus gratus gentilis Osgood

Peromyscus gratus gentilis Osgood, 1904, Proceedings Biological Society Washington, 17:61. Type from Lagos, Jalisco.
Peromyscus truei gentilis, Osgood, 1909, North American Fauna, 28:175.
Peromyscus truei truei, Hoffmeister, 1951, Illinois Biological Monographs, 21:30 (part).

Peromyscus gratus gratus Merriam

Peromyscus gratus Merriam, 1898, Proceedings Biological Society Washington, 12:123. Type from Tlalpan, Distrito Federal, Mexico.
Peromyscus truei gratus, Osgood, 1909, North American Fauna, 28:173.
Peromyscus sagax Elliot, 1903, Field Columbian Museum Publications 71, Zoological Series 3(8):142. Type from La Palma, Michoacan.
Peromyscus pavidus Elliot, 1903, Field Columbian Museum Publications 71, Zoological Series 3(8):142. Type from Patzcuaro, Michoacan.
Peromyscus zelotes Osgood, 1904, Proceedings Biological Society Washington, 17:67. Type from Querendero, Michoacan.

Peromyscus gratus zapotecae Hooper

Peromyscus truei zapotecae Hooper, 1957, Occasional Papers Museum Zoology, University Michigan, 586:6. Type from 1 mi E Tlacolula, 5700 ft., Oaxaca.

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